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Observations on the degree of stomatal movement in certain plants*

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The studies of Lloyd† and of Livingston‡ on the relation of stomatal changes to the rate of plant transpiration have rendered it very desirable that some quantitative information upon the opening and closing of stomata in a large number of plants be made available. Primarily, such knowledge should hasten the acquisition of some generalization upon the relation between stomatal changes and the daily march of water loss in plants, a generalization that seems to be utterly lacking at the present time.

We give, therefore, in the present paper, the results of a series of stomatal measurements on several different plant forms and at various hours of the day. Limitations in facilities and time prevented the testing of a larger number of forms as well as the undertaking of a study of the problem of stomatal influence upon transpiration as such; we have confined ourselves to an effort to determine approximately the degree of usual stomatal change which occurs between day and night under a somewhat widely representative complex of climatic conditions. The plants with which we have worked were all growing in the open soil in the recently established Botanical Garden of the Johns Hopkins University at Homewood, Baltimore, Maryland. The plants used were *Funkia ovata, Isatis tinctoria, Allium Cepa, Eichhornia speciosa,* and *Oenothera biennis.*

Following Lloyd's method,§ at various times of day and night samples of epidermis were stripped from the leaves without removal of the latter from the plants, and were quickly placed in absolute alcohol contained in suitable vials. Different but similar leaves of the same plant were used for any single series of observations. At a later time the samples were mounted in a solution of iodin in absolute alcohol and the determinations made microscopically. These consisted in finding the mean number of stomata occurring per unit area, on either side of the leaf, and measuring with ocular micrometer the length and breadth of the stomatal openings. Twenty stomata, taken at random, were measured in each case. It was found by repeated tests that the average result obtained from twenty stomata was not considerably altered by employing a larger number; a higher degree of accuracy than that here obtained would entail no great difficulty, but would be quite useless in the present state of our knowledge.

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* Botanical contribution from The Johns Hopkins University No. 27.

† Lloyd, F. E. The physiology of stomata. Publ. 89 Carnegie Inst. 1908.

‡ Livingston, B. E. Stomata and transpiration in *Tradescantia zebrina.* Science II. **29**: 269, 270. 1909.

§ Loc. cit. p. 26.

That the stomatal openings in the bits of epidermis fixed in alcohol by the method of Lloyd are generally unaltered by this treatment, is attested by Lloyd himself, by Miss S. Eckerson* and by Renner.† Since the method depends for its efficiency upon the rapidity with which the walls of the guard cells are dehydrated, it is clear that the reagent used must contain not more than a certain amount of water. We are not aware that this question of the requisite purity of the alcohol to be used in this sort of work has heretofore received attention in a quantitative way, and therefore present here the result of an extensive test in this regard, using the stomata of *Eichhornia* as subject. The bits of epidermis were placed in a series of "alcohols," ranging from absolute to 80 per cent (volume). We were surprised to discover that, for these stomata at least, 90 per cent alcohol was apparently as satisfactory for our purpose as was absolute. With over 10 per cent of water a slight closure of previously open stomata could be detected. With more than 20 per cent of water this induced closure was marked. In spite of these indications we persisted in the use of absolute alcohol for all the tests.

To bring out the method of handling the dimension data, TABLE I is presented. It includes the results of measurements of *Allium* stomata at 3:00 p. m. and at 12:30 a. m. Under each hour are first shown the actual dimensions, *a* and *b* (the long and short dimensions of the more or less elliptical cross sectional area

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* Eckerson, Sophia H. The number and size of stomata. Bot. Gaz. 46: 221–224. 22 S 1908.

† Renner, O. Beiträge zur Physik der Transpiration. Flora 100: 451–547. 1910.

TABLE I

Allium Cepa

August 30, 3:00 p. m.		August 31, 12:30 a. m.	
Dimensions of openings, *micra* ($a \times b$)	$\sqrt{ab}$	Dimensions of openings, *micra* ($a \times b$)	$\sqrt{ab}$
15 ×4.2	7.94		
15 ×6	9.49	12.6 ×3	6.15
15 ×6	9.49	12 ×4.5	7.35
15 ×6	9.49	Remainder	
15 ×6	9.49	closed	
15 ×5.7	9.25		
14.1 ×4.2	7.70		
15 ×4.2	7.94		
15 ×3.6	7.35		
13.5 ×3.9	7.26		
12.9 ×4.2	7.36		
12.9 ×4.5	7.62		
13.2 ×6	8.90		
14.1 ×4.5	7.97		
18 ×3.9	8.38		
12.6 ×4.8	7.78		
15 ×6	9.49		
12.9 ×4.5	7.62		
15 ×6	9.49		
12.9 ×5.1	8.11		
Mean $\sqrt{ab}$ (the index of relative diffusive capacity) is 8.40.		Mean $\sqrt{ab}$ (the index of relative diffusive capacity) is 0.685.	

of the stomatal pore). These are expressed in the form of an indicated product. In the second column of each series is shown the square root obtained, in each case, from the product of a and b. If we assume that the stomatal pore is elliptical in cross section, then the derived square root must represent the diameter of a circle with area equivalent to that of the ellipse in question. If minute elliptical openings allow the passage of diffusing gases at approximately the same rate as do circular openings of the same cross sectional area,* and also if such rates of gas diffusion through minute circular openings are proportional, not to cross sectional areas but to similar linear dimensions (as the diameters) of the openings;† then it follows that the square roots given in the table should be proportional, under otherwise identical conditions, to the rate of diffusion of water vapor through the corresponding stomatal pores. The studies of Brown and Escomb have left no doubt in regard to the validity of the principle of linear dimensions, as regards minute circular openings. The two assumptions, (1) that the configuration of the cross section of the stomatal pore nearly enough approaches that of an ellipse to permit the use of such calculations as ours, and (2) that diffusion through minute elliptical openings occurs at the same rate as through circular ones of the same cross sectional area, need further substantiation, but they are highly probable and at least carry us much further toward the inception of a quantitative knowledge of stomatal diffusive capacity than can any other method of treatment thus far available. While it is undoubtedly true that a stoma may close very considerably without at the same time producing alteration in the long axis of the ellipse, yet by the time closure is nearly completed that axis has shortened markedly in many plants. We are thus convinced that to assume the long axis as constant and compute diffusive capacities on the basis of the length of the short axis alone is a method not generally applicable.

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* Brown, H. T., and Escomb, I. Static diffusion of gases and liquids in relation to the assimilation of carbon and translocation in plants. Phil. Trans. Roy. Soc. London **193**: 283–291. 1900.

† Stefan, J. Versuche über die Verdunstung. Sitzber. K. Akad. Wiss. Wien, math. nat. Kl. **68**: 385–428. 1873. This contribution formed the point of departure for the work of Brown and Escomb (loc. cit.). See also, on this subject, Renner (loc. cit.).

If the square root of the product of the two elliptical axes may be taken as proportional to the diffusive capacities of the stomata involved, that is, to their power of transmitting water vapor, then the mean of the square roots derived from all measurements should be a relative measure of the average stomatal diffusive capacity at the hour of sampling. At the base of each part of TABLE I is given this mean.

It is seen at once from TABLE I that all stomata were open at the hour of daylight observation while the majority were closed at the night hour. The two open pores, out of twenty observed for the night hour, are seen to be less widely open than were any at the other time. All conditions being equal excepting that of the size of opening, the diffusive capacity of the stomata appears to be approximately 69/840, or 8.2 per cent as great at about midnight as at 3 in the afternoon.

In TABLE II are given the final results of the calculation for each case tested. Two series are presented, one carried out on August 30 and 31, the other on September 7 and 8, 1910. Besides the calculated diffusive capacities, are given the minima, means, and maxima of the actual dimensions. These latter are expressed as a series of three quantities, the middle one, in full face type, being the mean. The two series thus given for each hour represent, of course, the two axes of the stomatal ellipse. The number of stomata per square millimeter of leaf surface is given above the data in each case, excepting that of *Allium*, where it was not determined. *Funkia* has stomata only below and *Allium* has but one leaf surface to be considered.

It appears from our results that the diffusive capacity of the stomatal openings reached the zero point at night in all cases excepting *Allium*, *Eichhornia*, and the lower leaf surface of *Oenothera*. This is not to be taken as meaning even that stomatal transpiration actually ceased when the index of diffusive capacity, as here determined, vanished. There must always be some stomata that are SLIGHTLY open, and SOME diffusion undoubtedly may occur when closure is apparently complete. Of course, cuticular transpiration must continue whether the stomata are open or closed.

The greatest diffusive capacities are exhibited by the aquatic *Eichhornia*, and the stomata of this plant are clearly seen to alter

TABLE II

Funkia

Time of observation	Lower leaf surface (54 stomata per sq. mm.)	
	Dimensions of openings, *micra*	Index of relative diffusive capacity
Aug. 30 3:00 p. m.	0.6–**0.5**–3.0 × 10.0–**11.0**–15.0	3.93
6:30 p. m.	o×o	0.00
Aug. 31 12:30 a. m.	0.0–**0.27**–3.0 × 0.0–**1.0**–11.4	0.54
5:30 a. m.	0.0–**1.08**–4.5 × 0.0–**3.6**–15.0	1.95
10:00 a. m.	0.0–**1.3**–3.0 × 0.0–**6.5**–15.0	2.88

TABLE II—*Continued*

Isatis

Time of observation	Upper leaf surface (173 stomata per sq. mm.)		Lower leaf surface (182 stomata per sq. mm.)	
	Dimension of openings, *micra*	Index of relative diffusive capacity	Dimension of openings, *micra*	Index of relative diffusive capacity
Aug. 30 3:00 p. m.	0.0–**2.4**–4.5 × 0.0–**8.9**–13.5	4.56	0.0–**2.5**–4.8 × 0.0–**9.5**–15.0	4.77
6:30 p. m.	0 × 0	0.00	0.0–**0.15**–3.0 × 0.0–**0.45**–9.0	0.27
Aug. 31 12:30 a. m.	0 × 0	0.00	0 × 0	0.00
5.30 a. m.	0 × 0	0.00	0.0–**0.08**–1.5 × 0.0–**0.53**–10.5	0.21
10:00 a. m.	0.0–**0.66**–3.0 × 0.0–**2.1**–13.5	1.17	0.0–**2.2**–4.2 × 0.0–**9.9**–1.50	4.65

TABLE II—*Continued*

Allium Cepa

Time of observation	Dimensions of openings, *micra*	Index of relative diffusive capacity
Aug. 30 3:00 p. m.	3.6–**5.0**–6.0 × 12.6–**14.4**–18.0	8.40
6:30 p. m.	3.0–**4.2**–6.0 × 12.0–**13.0**–15.0	7.32
Aug. 31 12:30 a. m.	0.0–**0.38**–4.5 × 0.0–**1.23**–12.6	0.68
5:30 a. m.	3.0–**5.4**–7.5 × 9.0–**13.2**–15.6	8.37
10:00 a. m.	5.4–**7.5**–9.0 × 15.0–**19.3**–24.6	12.03

TABLE II—*Continued*

Eichhornia

Time of observation	Upper leaf surface (182 stomata per sq. mm.)		Lower leaf surface (91 stomata per sq. mm.)	
	Dimensions of openings, *micra*	Index of relative diffusive capacity	Dimensions of openings, *micra*	Index of relative diffusive capacity
Aug. 30				
3:00 p. m.	——	——	——	——
6:30 p. m.	9.0–**11.7**–12.0 × 18.0–**21.2**–24.0	15.75	4.8–**7.3**–9.0 × 22.5–**25.2**–27.6	13.53
Aug. 31				
12:30 a. m.	4.5–**7.5**–12.0 × 15.0–**19.8**–24.0	12.09	1.8–**5.6**–9.0 × 18.0–**23.1**–27.0	11.31
5:30 a. m.	4.5–**9.2**–11.4 × 18.6–**21.0**–24.0	13.89	3.9–**6.7**–12.0 × 20.1–**22.7**–27.0	12.27
10:00 a. m.	6.0–**11.1**–15.9 × 16.5–**22.8**–27.0	15.81	6.9–**10.1**–12.0 × 19.5–**22.6**–26.4	15.06

TABLE II—*Continued*

Oenothera biennis

Time of observation	Upper leaf surface (71 stomata per sq. mm.)		Lower leaf surface (364 stomata per sq. mm.)	
	Dimensions of openings, *micra*	Index of relative diffusive capacity	Dimensions of openings, *micra*	Index of relative diffusive capacity
Sept. 7				
1:00 p. m.	3.6–**5.1**–6.3 × 7.5–**10.0**–13.2	7.11	4.2–**5.55**–6.3 × 8.7–**10.9**–18.0	7.74
3:45 p. m.	3.0–**4.3**–6.0 × 6.3–**9.8**–15.0	6.42	0.0–**2.2**–5.1 × 0.0–**7.2**–12.9	4.23
6:20 p. m.	2.4–**3.3**–4.8 × 7.8–**10.4**–12.0	5.82	0.0–**1.6**–3.6 × 0.0–**6.5**–12.9	3.18
11:40 p. m.	0 × 0	0.00	0.0–**1.6**–3.0 × 0.0–**5.5**–12.0	2.91
Sept. 8				
5:40 a. m.	1.8–**3.8**–5.1 × 6.0–**9.2**–13.5	5.85	0.0–**2.3**–4.2 × 0.0–**6.7**–15.0	3.87
11:00 a. m.	3.0–**4.4**–6.0 × 6.0–**10.1**–15.0	6.63	1.8–**2.9**–4.5 × 6.3–**10.1**–12.6	5.34

their openings from day to night, though to a relatively slight degree. The diffusive capacity at night is about 12/16 (75 per cent) of its day magnitude for the upper leaf surface, and 11/15 (73.3 per cent) for the lower. Furthermore, *Eichhornia* possesses by far the largest daylight openings with which we have dealt. Next in order are *Allium* with an open capacity about half as great as in *Eichhornia*, and *Oenothera* with an open capacity somewhat less than that of *Allium*. *Funkia* and *Isatis* are not widely different from each other in the diffusive capacity of their open stomata, which is approximately half as great as that of *Allium*. A comparison of the amount and rate of stomatal closure, as exhibited by the two sides of the leaf, indicates that the upper stomata close and open more rapidly, or close more completely, than do the lower, though this difference is not pronounced in *Eichhornia*.

Many other points of interest are suggested by the data of TABLE II, but the time is not ripe for more detailed discussion; our aim in presenting these results has been merely to make a beginning in the acquisition of information upon which somewhat critical and quantitative studies may be based. It is hoped that others will attack this problem, so that the theory of stomatal effects may, as soon as may be, be brought to rest upon a more adequate foundation of actual measurements than is at present the case.

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